

Research Article

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Germination responses of the invasive hedge cactus (*Cereus uruguayanus*) to environmental factors

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Abstract

Hedge cactus (*Cereus uruguayanus* R. Kiesling; syn.: *Cereus hildmannianus* K. Schum.) is a columnar cactus that was introduced to Australia as an ornamental plant and has since become invasive in subhumid regions of Queensland and New South Wales. Compared with its congener, queen of the night (*Cereus jamacaru* DC.), which is currently invasive in both eastern and southern Africa, information on seed biology of *C. uruguayanus* is lacking. Experiments were conducted to study the effects of alternating day/night temperature, salt stress, water stress, and burial depth on germination and seedling emergence of four seed accessions of *C. uruguayanus*. Seeds were also subjected to a controlled aging test (CAT) to obtain an estimate of potential persistence under field conditions. The optimum temperature regime for germination of all accessions was 30/20 °C. Germination decreased with an increase in sodium chloride (NaCl) concentration, but germination of all accessions (range 26% to 81%) occurred at 160 mM NaCl, indicating very high salt tolerance. Seed germination gradually decreased with an increase in water stress, but germination in all accessions (range 19% to 47%) occurred at –0.8 MPa. Seed viability and dormancy status were unaffected by exposure to salt level (320 mM NaCl) and water (–1.6 MPa) stress under which germination did not occur. Germination responses to all three factors were generally similar to those documented for *C. jamacaru*. The emergence of *C. uruguayanus* decreased with an increase in seed burial depth. The highest emergence (43%) was recorded for surface-sown seeds, and emergence was reduced to 0 at a burial depth of 2 cm. CAT results for two seed accessions indicated that seeds of *C. uruguayanus* are likely to demonstrate extended (>3 yr) persistence under field conditions, a prediction that is supported by evidence that germination of its small (2-mm) seeds is markedly reduced by burial.

Introduction

The Cactaceae is a large family of succulent plants that comprises more than 120 genera and 1,500 species (Anderson 2001). Virtually all cacti are native to the Americas, but many species have been introduced around the world, either deliberately or accidentally (Nobel 2002). The intentional introductions have been cultivated for ornamental purposes, food, and various industrial uses. Some species have become major weeds across multiple countries, but all invasive cacti belong to only 5 of the 12 cactus growth forms, namely leaf-like, angled, cylindrical, flattened-padded, or sprawling (Novoa et al. 2015). Twenty-seven cactus species are listed as Weeds of National Significance in Australia, all of which belong to the Opuntioideae subfamily (flattened-padded growth forms) and the genera *Opuntia* and *Cylindropuntia* (Sheehan and Potter 2017). However, several species from other subfamilies are emerging or major weeds in Australia (Campbell et al. 2021).

Hedge cactus (*Cereus uruguayanus* R. Kiesling) is indigenous to southern Brazil, through Uruguay and to Argentina (Taylor and Zappi 2004) and was introduced to Australia for ornamental purposes. The plant is a columnar (cylindrical) cactus belonging to the Cactoideae subfamily and grows up to 6-m tall, forming a striking multistemmed, candelabra. It has been declared a priority pest species under local government legislation (Queensland Local Government Act 2009) in a number of regions of Queensland. Large infestations occur in the Central Highlands region and in southern inland Queensland, with smaller infestations scattered across southern/central Queensland (QDAF 2022). *Cereus uruguayanus* is also present in several locations in New South Wales (Hosking et al. 2007). It is most prevalent in mixed

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eucalypt–brigalow woodlands on light clay soils but also occurs in areas of cleared improved pasture and on a range of soil types (Campbell et al. 2021). In South Africa, the mealybug, *Hypogeococcus* sp. (Pseudococcidae) has brought infestations of the congeneric queen of the night (*Cereus jamacaru* DC.) under control within 10 yr of its release (Paterson et al. 2021). *Hypogeococcus pungens* was originally introduced in Queensland to control another invasive cactus, moon cactus (*Harrisia martini* (Labour.) Britton), but has spread spontaneously to *C. uruguayanus* where the two cacti co-occur. It has caused a degree of plant mortality in *C. uruguayanus* and has been moved actively to other infestations of this species (C Hunter, personal communication). It is too early to determine whether *H. pungens* will exert effective biological control against *C. uruguayanus*.

The primary mode of reproduction in members of the Cactoideae is through seeds, as compared with many other weedy cacti, in which vegetative reproduction also contributes to population buildup and spread (Paterson et al. 2021). Very little information is currently available on the seed biology of *C. uruguayanus*, but the closely related *C. jamacaru* is well studied. The latter species is native to northeastern Brazil and has been recorded as being invasive in Kenya (Witt and Luke 2017) and being a transformer, namely a weed that has changed the character, condition, form, or nature of an ecosystem over substantial areas relative to its extent (Richardson et al. 2000), in South Africa (Henderson 2001). Investigations have been conducted into the effects of a number of factors on *C. jamacaru* germination, including light (Abud et al. 2013; Alencar et al. 2012), temperature (Abud et al. 2013; Alencar et al. 2012), water stress (Meiado et al. 2010; Ortiz et al. 2019; Silva and de Azerêdo 2022), salt stress (Meiado et al. 2010; Silva and de Azerêdo 2022), and pH (Ortiz et al. 2019). Results from these studies indicate that the optimum temperature for germination in *C. jamacaru* is between 25 and 30 C and that germination is susceptible to both water and salt stress.

Persistence of weed seeds in the soil is a major determinant of the cost and duration of weed control activities (Brooks et al. 2022). Traditional methods for estimating weed seed persistence, such as repeated field soil sampling and buried packet trials, can take many years and require substantial resourcing (Brooks et al. 2022; Panetta 2004). The controlled aging test (CAT; in which seeds are maintained under conditions of constant high temperature and humidity) accelerates the aging process and can provide reasonably reliable estimates of field seed persistence, at least in terms of the broad categories of transient (<1 yr), short-lived (1 to 3 yr), and long-lived (>3 yr) (Long et al. 2008).

The aims of the present investigation were to: (1) evaluate the effects of alternating day/night temperature, salt stress, and water stress on *C. uruguayanus* germination, plus the effect of burial depth on its seedling emergence; (2) determine whether any of these responses varied between seeds sampled from different accessions of *C. uruguayanus*; and (3) employ the CAT to obtain a first-pass estimate of potential seed persistence of this weed.

Materials and Methods

Seed Collection and Processing

Fruits of *C. uruguayanus* were collected during the period of January/February 2022. Only mature fruits (i.e., those that were pinkish red to red) were collected. Four collections were made in Queensland: near Inglewood (28.43°S, 150.97°E), Sapphire

(23.46°S, 147.72°E), Willows (23.74°S, 147.54°E), and Plainland (27.56°S, 152.42°E). The Inglewood site was located along a road verge that was ungrazed, except for occasional periods associated with movement of cattle from one destination to another. Both the Sapphire and Willows sites were in areas designated for gem fossicking and were consequently highly disturbed, with occasional grazing—mainly by cattle but also occasionally by feral camels at Sapphire. The Plainland site was a vacant allotment in a semi-urban area. It had been previously cleared, with isolated remnant trees and a scattering of mature *C. uruguayanus* plants growing in close proximity to them. None of the sites had a history of control activity targeting *C. uruguayanus*.

The extraction of seeds was carried out by opening the fruits and removing the pulp by maceration in a colander and rinsing under running water. The seeds were then dried and stored at room temperature (25 ± 2 C) until used in the experiments.

General Protocol

Experiments were conducted from March 2022 to January 2023. With the exception of Experiment 5, all experiments were repeated, with the second run commencing within a month of the completion of the first run. In each run, there were 3 replicates of 25 seeds per unit (whether petri dish or pot), except for the CAT, in which 50 seeds were used. Each petri dish was 9 cm in diameter and contained a double layer of Whatman No. 1 filter paper (Cytiva, Paramatta, NSW, Australia). Each dish received 5 ml of either water or the relevant solution, and dishes were placed in sealed plastic bags to reduce evaporation. Salt and water potential experiments were conducted at 30/20 C (12-h light/12-h dark, 85 μmol m⁻² s⁻¹ light intensity), because this temperature and degree of illumination were found to be optimal in Experiment 1. Labec incubators (Labec Laboratory, Marrickville, Sydney, NSW, Australia) were used for the temperature-, salt-, and water-stress experiments.

Experiment 1. Effect of Alternating Temperature on Germination

The experiment had a 5 by 4 factorial design, with five levels of temperature (15/5, 20/10, 25/15, 30/20, or 35/25 C) and four sites of seed origin (as per “Seed Collection and Processing”). The temperature regimes are typical of the seasonal variation that occurs in Queensland, particularly under conditions where soil moisture might be sufficient to promote germination. The light regime was 12-h light/12-h dark, and germination was scored every week for 5 wk.

Experiment 2. Effect of NaCl on Germination

The experiment had a 6 by 4 factorial design, with six levels of salinity (0, 20, 40, 80, 160, or 320 mM NaCl) and four sites of seed origin (as per “Seed Collection and Processing”). This range of salinity is representative of the variation in soil salinity that can be found in Australian soils (Rengasamy 2002). Germination was scored after 3 wk, as results from Experiment 1 showed that there was no germination after this point in seeds maintained at 30/20 C. Ungerminated seeds at the highest salt concentration (320 mM NaCl) were then washed with water and incubated again in water for 3 wk to determine whether seeds were still viable.

Experiment 3. Effect of Water Potential on Germination

The experiment had a 6 by 4 factorial design, with six levels of osmotic potential (0, -0.1, -0.2, -0.4, -0.8, and -1.6 MPa) and

four sites of seed origin (as per “Seed Collection and Processing”). Solutions were prepared using polyethylene glycol (PEG) 8000 (Sigma-Aldrich, St Louis, MO, USA) following the procedure described by Michel and Radcliffe (1995). Germination was scored after 3 wk. As in Experiment 2, ungerminated seeds at the lowest osmotic potential (−1.6 MPa) were washed with water and incubated again in water for 3 wk.

Experiment 4. Effect of Burial Depth on Germination and Emergence

The experiment had a 6 by 4 factorial design, with six depths of burial (0, 0.5, 1, 2, 4, or 8 cm) and four sites of seed origin (as per “Seed Collection and Processing”). Seeds were sown in 20-cm-diameter plastic pots (25 seeds per pot), using field soil from Gatton Farms. The soil used was a clay loam in texture with organic matter composition of 2.7% and a pH of 7.2. Pots were placed in a screenhouse and subsurface irrigated. The number of seedlings was counted 4 wk after commencement (in October 2022 for the first run and December 2022 for the second run) of the experiment.

Experiment 5. CAT

Seeds from fruits collected at Willows and Plainland were extracted and stored at laboratory temperature until used. Seed lots (50 seeds each) were subjected to a “hydration” phase, then an “aging” phase, following the protocol of Hay et al. (2006). Each CAT batch used two replicate IP67 electrical boxes (labeled A and B). Seed lots were placed in individual open glass vials, half in each of the sealed boxes. For the hydration phase, lots were exposed to 47% relative humidity over a lithium chloride solution (320 g L^{−1} H₂O) in a dark 20 C Thermoline[®] incubator (Wetherill Park, NSW, Australia) for 14 d. A reference sample of 50 seeds from each seed lot was removed from boxes A and B and incubated (see below) before the aging phase (day 0). For the aging phase, the temperature was increased to 45 C with 60% relative humidity (lithium chloride at 370 L^{−1} H₂O). Seeds remained in the aging environment for 2 to 126 d. At each time of retrieval (2, 7, 14, 21, 28, 35, 42, 56, 77, 98, and 126 d), seeds were removed and placed on moistened filter paper over an inverted watch glass in a 90-mm petri dish. Petri dishes were kept moist with distilled water in a Thermoline[®] incubator running at a 30/20 C 12-h diurnal cycle, and germination was recorded twice weekly until no further germination was observed. Test conditions were checked with Onset[®] Hobo[®] temperature and humidity loggers (Notting Hill, VIC, Australia), and the lithium chloride solution was adjusted as necessary. This test provides only a rough estimate of potential persistence of seeds under field conditions, which can be expected to vary considerably due to variation in soil type, rainfall incidence, and temperature. Given the intrinsic limitations of the approach, we considered that results from a single experiment would be sufficiently informative.

Statistical Analyses

Experiments 1 to 4 were conducted in a completely randomized design (factorial). All experiments were repeated over time and each run had three replications for each treatment. Data were subjected to ANOVA using Genstat-combined analysis. Data were combined over the two runs, as there was no interaction between the runs and treatments, and the run effect was not significant. Figures were plotted using SigmaPlot v. 14.5.

For Experiment 5, germination of the aged seed was calculated as a proportion of the day 0 germination (proportion viable = 1 at

day 0) per box. Proportion germinable data over time in the A and B boxes were used to chart a negative logistic regression curve in Genstat[®] v. 22 (VSN International, Hemel Hempstead, UK):

$$G = a + c/[1 + e^{-b(x-m)}] \quad [1]$$

where G represents the germinable proportion of seeds remaining at time x ; c is the fitted initial viability; b is the slope decay; a represents the vertical shift/asymptote of the sigmoid curve; and $m = T_{50}$, the time taken for the germinable proportion to fall to 50%.

Results and Discussion

Effect of Alternating Temperature on Germination

The maximum germination obtained under any temperature regime was 99%. The optimum regime was 30/20 C (i.e., 25 C mean temperature) (Figure 1). Here, the average germination was 95%, with no statistically significant differences among accessions. In consequence, Experiments 2 to 4 were conducted under this condition. This germination response to temperature is identical to that previously observed for *C. jamacaru*, where the optimum temperature was constant 25 C (Abud et al. 2013) or constant 25 or 30 C (Alencar et al. 2012). A significant interaction (P-value < 0.05) was detected between accession and temperature, likely due to the reduction in cumulative germination at 35/25 C in the Plainland and the Sapphire accessions. Irrespective of accession, no germination occurred at the lowest temperature regime (15/5 C), indicating that germination of *C. uruguayanus* is less likely to occur during winter. Seeds germinated at 20/10 C, suggesting that some germination may occur during relatively mild winters, particularly during sporadic warm spells.

In a review of seed traits and germination in the Cactaceae, Barrios et al. (2020) found that the majority of taxa demonstrate optimal germination between 25 and 30 C. This generalization largely holds within the genus *Cereus*, but some variation between species has been reported. At constant temperatures, maximum germination for *C. hildmannianus* was found at 20 and 25 C (Becker et al. 2020), for *Cereus hankeanus* F.A.C. Weber ex K. Schum., at 25 C (Lindow-López et al. 2018), and for *Cereus fernambucensis* Lem. and *Cereus albicaulis* (Britton & Rose) Luetzelb., at 25 and 30 C, respectively (Meiado et al. 2016). The optimum constant temperatures for germination of *Cereus pernambucensis* Lem. ranged between 25 and 35 C, with no differences observed under alternating temperature regimes between 30/20 C and 35/30 C (Socolowski et al. 2010). However, for *C. fernambucensis*, germination was reduced under alternating temperatures relative to the equivalent mean temperature, that is, maximum germination occurred under constant 25 C but “greater than 50% germination” was observed at 30/20 C (Meiado et al. 2016).

Effect of NaCl on Germination

Seeds of *C. uruguayanus* are highly tolerant to salt stress (Figure 2), as evidenced by germination in all seed accessions at 160 mM NaCl—considered to be a very saline condition (Abrol et al. 1988). Soils with an NaCl concentration of 20 mM are considered to be salt affected, and in Queensland alone, an area of more than 100,000 ha is saline (Trewin 2002). A highly significant interaction (P-value < 0.001) was detected between accession and treatment, likely due to the substantial reduction in cumulative germination at

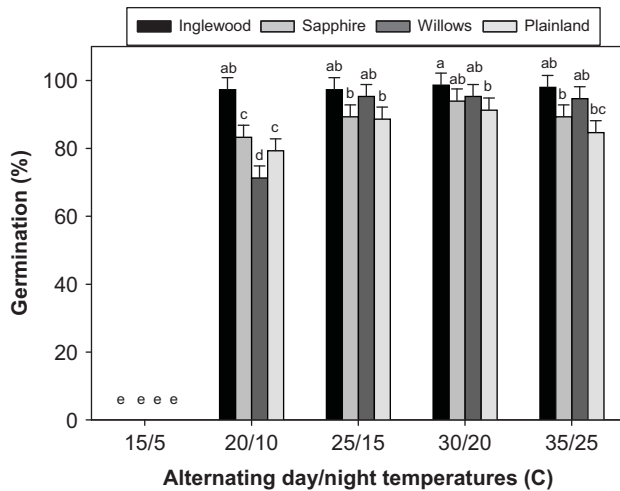


Figure 1. Effect of alternating day/night temperature regimes on the cumulative germination of four seed accessions of *Cereus uruguayanus*. Values with the same letter do not differ at a 5% level of significance.

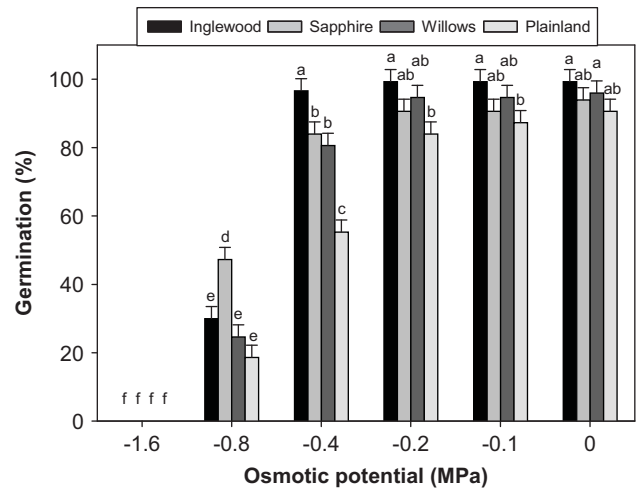


Figure 3. Effect of water stress on the cumulative germination of four seed accessions of *Cereus uruguayanus*. Values with the same letter do not differ at a 5% level of significance.

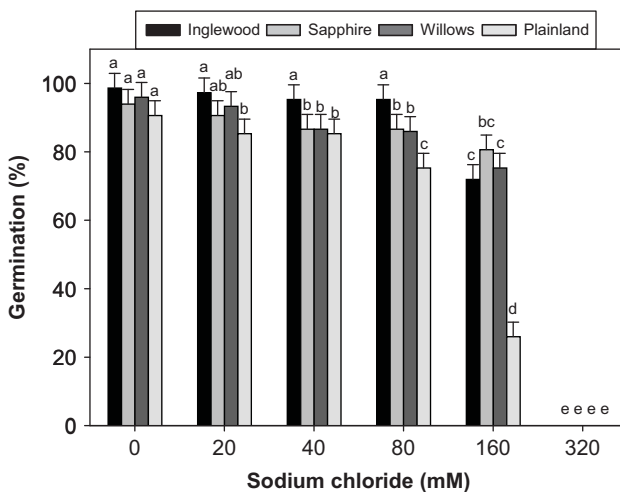


Figure 2. Effect of salt stress on the cumulative germination of four seed accessions of *Cereus uruguayanus*. Values with the same letter do not differ at a 5% level of significance.

160 mM NaCl in the Plainland accession. When seeds from the 320 mM treatment were washed and again incubated with water, germination was similar (91% to 99%) to that of the control, indicating that salt did not affect seed viability or germinability. This suggests that seeds are not damaged by exposure to high salinity and could persist until there was rainfall (or flooding) sufficient to reduce salinity to a level that did not impede germination.

Reductions in germination of *C. jamacaru* were not detected until NaCl concentrations reached 160 mM (Meiado et al. 2010; Silva and de Azerêdo 2022), with germination observed even at 200 mM (Meiado et al. 2010). This raises the possibility that *C. uruguayanus* is even more tolerant to salt stress than could be detected under the present experimental conditions.

Other studies on columnar cacti have not examined the effects of NaCl per se on germination. Rather, they have focused on germination responses to different water potentials that are established by using NaCl concentrations that have not been specified.

Effect of Water Potential on Germination

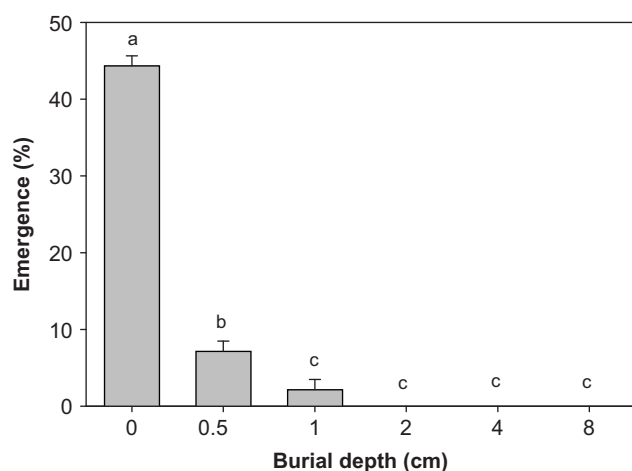
Seeds of *C. uruguayanus* were also highly tolerant to water stress, with most accessions achieving germination levels of 80% or higher at -0.6 MPa and germination of all accessions occurring at -0.8 MPa (Figure 3). There was a highly significant interaction (P -value < 0.001) between accession and treatment, likely due to the higher tolerance exhibited by the Sapphire accession. (The reductions in germination between -0.4 MPa and -0.8 MPa were 70%, 44%, 69%, and 66% for the Ingleswood, Sapphire, Willows, and Plainland accessions, respectively). When seeds from the -1.6 MPa treatment were washed and again incubated with water, germination was similar (90% to 99%) to that of the control, suggesting that water stress did not affect viability or germinability of the seeds, as was found for salt stress in Experiment 2. Seeds of *C. jamacaru* demonstrated a similar level of tolerance to water stress in the study by Silva and de Azerêdo (2022), with germination remaining unaffected at an osmotic potential of -0.6 MPa. However, substantial reductions occurred between -0.6 MPa and -0.8 MPa. Conversely, Meiado et al. (2010) reported that *C. jamacaru* exhibited a much higher degree of sensitivity to water stress, with reductions in germination beginning at -0.2 MPa and minimal germination observed at -0.6 MPa and -0.8 MPa. It is worth noting that Silva and de Azerêdo (2022) calculated osmotic potentials from NaCl concentrations using the Van't Hoff equation (Salisbury and Ross 1991), whereas Meiado et al. (2010) established solutions with different osmotic potentials by varying PEG concentrations, mirroring our approach in this research. This suggests that the latter method might be more appropriate for evaluating the germination response to water stress. Meiado et al. (2010) postulated that *C. jamacaru* seeds possess the ability to absorb or metabolize salt for other purposes, potentially explaining their ability to germinate at such high salt concentrations.

Barrios et al. (2020) observed that germination of other columnar cactus species occurred at water potentials of -0.2 MPa (Flores et al. 2017; Guillén et al. 2009), -0.4 MPa (Flores and Briones 2001; Flores et al. 2017; Guillén et al. 2011), or even -0.6 MPa (Flores and Briones 2001). However, they noted that water potentials lower than -0.6 MPa generally significantly reduced germination (Flores et al. 2017; Guillén et al. 2011).

Table 1. Seed survival of two *Cereus uruguayanus* accessions under controlled aging at 60% relative humidity and 45 C.^a

Seed accession	Parameter estimates (\pm SE)				R^2
	<i>a</i>	<i>b</i>	<i>c</i>	<i>m</i>	
Plainland	0.019 (0.029)	-0.106 (0.016)	0.960 (0.0387)	55.72 (1.61)	97.9
Willows	0.025 (0.047)	-0.079 (0.012)	0.974 (0.054)	79.81 (2.30)	97.5

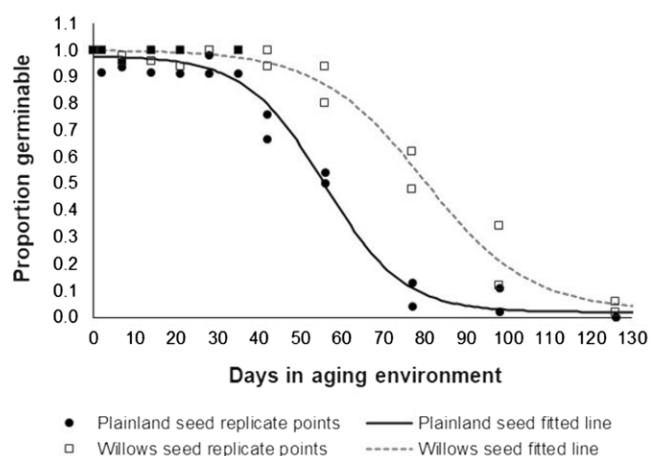
^aA negative logistic regression model, $G = a + c/[1 + e^{-b(x-m)}]$, was fit to the seed survival data. In the equation, *G* represents the germinable proportion of seeds remaining at time *x*; *c* is the fitted initial viability; *b* is the slope decay; *a* represents the vertical shift/asymptote of the sigmoid curve; and *m* = T_{50} , the time taken for the germinable proportion to fall to 50%.

**Figure 4.** Effect of burial depth on seedling emergence of *Cereus uruguayanus*. Values with the same letter do not differ at a 5% level of significance.

Given the low absolute seedling growth rates observed for *C. jamacaru* (Abud et al. 2013), which is likely to be the case as well for *C. uruguayanus*, recruitment of both species probably can occur only under scenarios of extended high moisture availability. These could include major single-rainfall events and/or closely spaced sequences of smaller events.

Effect of Burial Depth on Germination and Emergence

Seed accessions did not differ significantly in their responses to burial depth, and because the interaction between accession and burial depth was not significant, data were combined over accessions. Maximum emergence occurred from seeds that were surface sown, and emergence declined markedly with increases in burial depth—no emergence occurred from 2 cm or deeper (Figure 4). Seeds of *C. jamacaru* have been variously reported to be neutrally (Abud et al. 2013) and positively (Alencar et al. 2012) photoblastic. The latter authors reported germination in constant darkness of 72%, 67%, and 67% for *C. jamacaru* seeds maintained at 20, 20/30, and 25 C, respectively. We have not determined the germination response of *C. uruguayanus* to light per se. However, markedly lower emergence from seeds that were buried at 0.5 cm suggests that a major component of a *C. uruguayanus* seed population may have a light requirement, given the strong germination response under intermittent light and fluctuating temperature (Figure 1). A smaller proportion could respond to alternating temperature, with roughly 7% emergence from 0.5 cm and 2% from 1.0 cm (Figure 4). Regardless, the substantial reduction of emergence associated with shallow burial indicates

**Figure 5.** Seed survival of two *Cereus uruguayanus* accessions under controlled aging at 60% relative humidity and 45 C. Parameter estimates for the negative logistic regression model fit to the data are given in Table 1.

that burial may enforce dormancy in seeds of *C. uruguayanus*, thus providing a mechanism for promoting seed persistence.

CAT

Results from the aging test suggest that *C. uruguayanus* seeds are not likely to be short-lived under field conditions, with T_{50} values of 55.7 and 79.8 d for the Plainland and Willows accessions, respectively (Table 1; Figure 5). Long et al. (2008) reported that species associated with an extended field persistence (> 3 yr) exhibited T_{50} values of >50 d under CAT conditions. Potential enforcement of dormancy via burial of the small (2-mm) seeds of *C. uruguayanus* should also promote seed persistence. The higher T_{50} value for the Willows accession indicates that infestations in this area may require longer periods of active management in the absence of seed input than might be the case for those around Plainland.

For *C. uruguayanus*, the optimum temperature regime for all accessions was 30/20 C. Seed germination percentages decreased with an increase in NaCl concentrations, but germination of all accessions occurred at 160 mM NaCl, indicating very high salt tolerance. Similarly, germination levels gradually decreased with an increase in water stress, but germination of all accessions occurred at -0.8 MPa. Germination responses of *C. uruguayanus* were, for the most part, similar to those documented for the closely related *C. jamacaru*.

Significant interpopulation differences in the germination responses of *C. uruguayanus* were found in two of its seed accessions: Sapphire (S) and Plainland (P). Such variation

comprised greater than average reduction in germination at the highest temperature regime (S and P); higher than average reduction in germination in response to salt stress (P); and lower than average reduction in response to water stress (S). It would be difficult to make a case for local adaptation on the basis of these limited results. Equally, the implications, if any, for management are unclear, because it is unknown whether the differences that we observed in germination would be reflected at the recruitment stage. That said, the potential for range expansion (and infill) of *C. uruguayanus* within Australia is apparent—being supported by the prevalence of animal-vectored seed dispersal in the genus *Cereus* (see Gomes et al. [2014] for documentation of frugivory and seed dispersal of *C. jamacaru*), germination over a broad range of environmental conditions, and the likelihood of persistence via the soil seedbank.

Future research on *C. uruguayanus* should include an examination of the effects of temperature, as well as salt and water stress, on seedling growth. Field observations on soil seed dynamics are required to test the prediction of extended seed persistence for the species.

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The authors declare no competing interests.

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